33. The External Characters of the Koala (*Phascolarctos*) and some related Marsupials. By R. I. Pocock, F.R.S., F.Z.S.

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(Text-figures 22–26.)

Contents.

Introduction.

The body of the female *Phascolarctos* described in the following paper was very kindly sent to me by Mr. A. F. Richardson when I explained to him the zoological importance of the animal and the infrequency with which fresh examples come into the hands of anatomists in this country.

The need for renewed examination of *Phascolarctos* is especially shown by the disagreement amongst modern zoologists regarding the position and status to be assigned to it in the classification of Diprotodont Marsupials. Thomas, for instance (Cat. Marsupialia and Monotremata in Brit. Mus. 1888), divided the suborder into three families: (1) Macropodidæ with the subfamilies Macropodinæ, Potoroinæ, Hypsiprymnodontinæ; (2) Phalangeridæ with the subfamilies Tarsepedinæ (*Tarsipes*), Phalangerinæ (*Phalanger*, *Trichosurus*, *Pseudochirus*, *Petauroides*, etc.), and Phascolarctinæ (*Phascolarctos*); and (3) Phascolomyidæ (*Phascolomys*).

In connection with the Macropodidæ and Phalangeridæ, Thomas pointed out that the characters of *Hypsiprymnodon* are intermediate between those of the two families, and render the division between them by no means so sharp and well-defined as it has been usually considered to be. Nevertheless, his arrangement suggests that *Phascolarctos* is an aberrant member of the Phalangeridæ more nearly related to *Phalanger* than the latter is to *Macropus*.

Thomas's classification has been adopted by English zoologists and by Trouessart in his Catalogue (1912).

Bensley (Amer. Nat. xxxv. pp. 117–138 and 245–269, 1901; and Tr. Linn. Soc. Lond. (2) ix. pt. iii. pp. 83–214, 1903) followed Thomas in admitting the family Phascolomyidæ and in regarding *Phascolarctos* as the representative of a subfamily of the Phalangeridæ; but he made the important modification of transferring

Pseudochirus and *Petauroides* from the Phalangerinæ to the Phascolarctinæ because of the crescentic (subselenodont) pattern of the molar teeth in the three genera. Bensley's classification was adopted, presumably with approval, by W. K. Gregory (Bull. Amer. Mus. Nat. Hist. xxvii. pp. 215–216, 1910), who was acquainted with but rejected the classification by Winge quoted below.

Thomas, of course, was quite familiar with the dental character to which Bensley and Gregory attached so much importance. On p. 167 of his Catalogue he pointed out that by the complicated subselenodont character of its molars, *Pseudochirus*, with its close ally *Petauroides*, stands somewhat apart from most of the other Phalangers, and approaches *Phascolarctos*, in which a similar but simpler modification is observable. But his reasons for attaching to it subordinate systematic value lay apparently in the circumstance that in young examples of *Phalanger* a tendency towards the same structure is visible, but the crests on the molars soon wear off, leaving little difference between them and the simple quadricuspid molars characteristic of typical genera of Phalangeridæ. The obvious, but not on that account necessarily true, inference to be drawn from this fact is that the tendency towards the subselenodont molar pattern exhibited by *Phalanger* is a primitive character of the family Phalangeridæ, which is temporarily retained in *Phalanger*, lost in *Trichosurus*, *Dactylopsila*, and others, and elaborated in *Pseudochirus* and *Phascolarctos*.

Winge (E Museo Lundii, viii. pt. 1, 1893) held very different views. He adopted two families: (1) Phalangistidæ [=Phalangeridæ] with the subfamilies Pseudochirini for *Pseudochirus* and *Petauroides*, and the Phalangistinæ [=Phalangerinæ] for the two groups Phalangistæ (*Phalanger*, *Trichosurus*, *Petaurus*, *Tarsipes*, etc.), and Macropodes (*Macropus*, *Hypsiprymnodon*, etc.); (2) Phascolarctidæ with the subfamilies Phascolarctini (*Phascolarctos*) and Phascolomyini (*Phascolomys*)*.

Winge took as the basis for his classification the degree of extension of the tympanic process of the alisphenoid, which in the Phascolarctidæ (*Phascolomys*, *Phascolarctos*) is small, does not envelope the tympanic cavity, and fails to reach the paroccipital process, whereas in the Phalangeridæ, comprising the rest of the genera of Diprotodont Marsupials, the bone in question is large, envelops the tympanic cavity, and reaches the paroccipital process. As accessory characters, the vestigial tail, the presence of a cardiac gland in the stomach, and the loss of one of the two normal pairs of teats further serve to distinguish the Phascolarctidæ from the Phalangeridæ†.

* To these Winge added Thylacoleontini (*Thylacoleo*) related to Phascolarctini and Diprotodontini (*Diprotodon*, *Nototherium*) related to Phascolomyini.

† Winge's valuable paper is unfortunately written in Danish. The statements about the extension of the alisphenoid is taken from Max Weber's work. I have not been able to verify it in the case of the two skulls of *Phascolarctos* available for examination.

Attention may also be drawn to Winge's severance of the crescent-toothed or subselenodont Phalangers (*Pseudochirus* and *Petauroides*) from the rest as representing a special subfamily Pseudochirini equivalent to the Phalangerinæ containing not only the rest of the genera Thomas assigned to that subfamily, but all of those constituting the family Macropodidæ of that author.

Max Weber (Die Säug. p. 348, 1904) followed Winge in admitting the two families Phalangeridæ and Phascolarctidæ as he defined them; but he did not admit the subfamily groups Phascolarctinæ and Phascolomyinæ for *Phascolarctos* and *Phascolomys* respectively, and in the case of the Phalangeridæ he made a compromise between Thomas's and Winge's systems by dividing the family into three subfamilies: Phalangerinæ, Hypsiprymnodontinæ, and Macropodinæ.

It will be noticed that neither Winge nor Max Weber attaches any particular importance to the structural peculiarities of *Tarsipes*.

The divergence of opinion between the authors quoted may be briefly and more clearly expressed by the following tabulation of their classifications:—

Thomas. Family MACROPODIDÆ.
- Subfamily MACROPODINÆ (*Macropus, Dendrolagus*, etc.).
- „ POTOROINÆ (*Potorous, Bettongia*, etc.).
- „ HYPSIPRYMNODONTINÆ (*Hypsiprymnodon*).

Family PHALANGERIDÆ.
- Subfamily TARSIPEDINÆ (*Tarsipes*).
- „ PHALANGERINÆ (*Phalanger, Trichosurus, Pseudochirus, Petauroides*, etc.).
- „ PHASCOLARCTINÆ (*Phascolarctos*).

Family PHASCOLOMYIDÆ (*Phascolomys*).

Bensley. Family MACROPODIDÆ (*Macropus, Hypsiprymnodon*, etc.).
- „ PHALANGERIDÆ.
- Subfamily TARSIPEDINÆ (*Tarsipes*).
- „ PHALANGERINÆ (*Phalanger, Trichosurus*, etc.).
- „ PHASCOLARCTINÆ (*Pseudochirus, Petauroides, Phascolarctos*).

Family PHASCOLOMYIDÆ (*Phascolomys*).

Winge. Family PHALANGERIDÆ *.
- Subfamily PHALANGERINÆ.
- *a*. Macropodes (*Macropus, Hypsiprymnodon*, etc.).
- *b*. Phalangeri (*Tarsipes, Phalanger, Trichosurus*).
- Subfamily PSEUDOCHIRINÆ (*Pseudochirus, Petauroides*).

Family PHASCOLARCTIDÆ.
- Subfamily PHASCOLARCTINÆ (*Phascolarctos*).
- „ PHASCOLOMYINÆ (*Phascolomys*).

* For the sake of clearness in comparison, I have here altered the name *Phalangista* and its derivatives used by Winge to *Phalanger* and its derivatives.

Weber. Family PHALANGERIDÆ.
Subfamily MACROPODINÆ (*Macropus, Dendrolagus, Potorous, Bettongia*, etc.).
„ HYPSIPRYMNODONTINÆ (*Hypsiprymnodon*).
„ PHALANGERINÆ (*Tarsipes, Phalanger, Trichosurus, Pseudochirus, Petauroides*).

Family PHASCOLARCTIDÆ (*Phascolarctos, Phascolomys*).

External Characters.

The Rhinarium.—In *Trichosurus* the rhinarium is large, naked, and convex above; the infranarial portions are complete laterally and narrow; there is a median groove extending between the nostrils on to the philtrum, which is divided into two narrow strips, with a little process, overlying the gum between the median incisors, at the apex of the angular excision above. The nostrils are of the typical form, consisting of a rounded orifice in front, moderately widely separated from its fellow of the opposite side, and of a lateral and posterior narrow slit.

In *Phalanger* the rhinarium is in a general way similar to that of *Trichosurus*, but the nostrils are more widely separated, the infranarial portion is deeper in front, and the philtrum is exceedingly wide, and, although gradually narrowed below, is quite wide where it terminates on the edge of the upper lip. There is, moreover, no angular excision such as is seen in *Trichosurus*, but the median groove broadens below, its floor terminating in a median process which projects at least as low as the lateral portions of the philtrum.

In *Pseudochirus* the rhinarium is more like that of *Trichosurus*, but the infranarial portions are wider in front, with the inferior edge more steeply inclined; the median groove is continued between the nostrils to the summit of the rhinarium; and the inferior portion of the philtrum is quite narrow, with a small median notch.

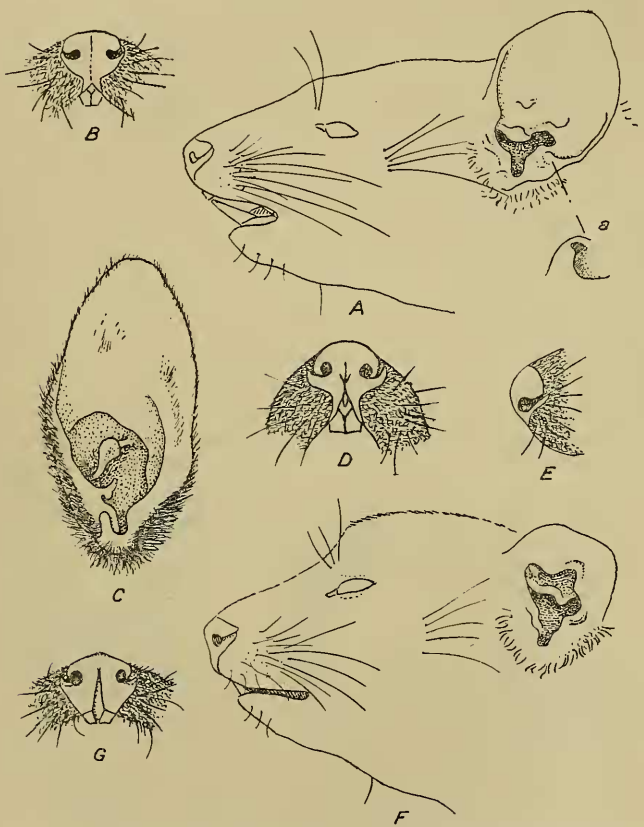
In *Phascolarctos* the nose is widely different. The muzzle is abruptly sloped downwards about an inch above the nostrils, and the whole of this inclined area is covered with very fine, short, scattered hairs, leaving a narrow, naked, thickened rim round the nostrils. Thus there is no true rhinarium. The nostrils themselves are also peculiar. Each consists of an ovally elongated valvular orifice, with a thickened superior and lateral rim, but with the inferior rim hardly defined from the upper lip; all trace of differentiation into lateral slit and anterior orifice has disappeared; the septum is very narrow, and is continued inferiorly between the two halves of the upper lip, ending below in a process over the gum between the median incisors.

In *Phascolomys ursinus* * the rhinarium is quite unlike that of *Phascolarctos*, and resembles, broadly speaking, the rhinarium

* The rhinarium of *Lasiorhinus latifrons*, the hairy-nosed Wombat, which should, I think, rank as a distinct genus, is unknown to me except from descriptions and a dried skin. It appears to differ solely from that of *Phascolomys* in being covered with short hair, the nostrils being normally formed.

of the three genera of Phalangers above described. It extends dorsally, however, further backwards in the middle line, and the hair of the muzzle encroaches over the well-developed slit of the nostrils, the expanded portions of which are widely separated in the middle line. The infranarial portions are moderately deep, and reach almost to the posterior end of the nostril-slits.

Text-figure 22.



A. Head of *Pseudochirus peregrinus*, with pocket of ear (*a*) seen from above.
B. Rhinarium of the same.
C. Ear of *Trichosurus vulpecula*.
D. Rhinarium of the same, from the front.
E. Rhinarium of the same, from the side.
F. Head of *Phalanger maculatus*, the ear stripped of hair.
G. Rhinarium of the same, from the front.

Their inferior edge slopes obliquely downwards and inwards to the gum of the incisors, the two lobes of the upper lip being

tolerably widely separable at this point. There is no median excision in the inferior edge of the rhinarium above the teeth, and there is no median groove, but a groove runs on each side from the nostril downwards and inwards to the gum, defining the infranarial portion from the rest of the rhinarium.

Facial Vibrissæ.—The facial vibrissæ are well and normally developed in *Trichosurus*, *Phalanger*, *Pseudochirus*, and *Phascolomys*, being represented by numerous long mystacials, superciliaries, genals—one tuft,—submentals, and interramals. In the examples of *Phalanger* and *Pseudochirus* examined, however, the interramals were few in number and slender. In *Phascolarctos* the vibrissæ are comparatively poorly developed, the mystacials especially being few and short and the interramal tuft wanting.

The Mouth.—There are only two points for me to notice in connection with the mouth. The first is the presence, with which everyone is familiar, of cheek-pouches in *Phascolarctos*. These lie alongside the gum of the upper jaw in front, the orifice looking downwards and the cavity extending upwards and backwards towards the eye. No such pouches occur in *Trichosurus*, *Phalanger*, *Pseudochirus*, or *Phascolomys*. The second is the presence in *Phascolomys* of a flap of naked skin extending into the mouth from the inner surface of the lips laterally. This is analogous to the similar ingrowths well known in the Rodentia, where they serve to close the throat during gnawing. Their function is no doubt the same in *Phascolomys*, which has rodent incisor teeth. These oral flaps of skin are not developed in the other genera here discussed, nor so far as I am aware in any other Marsupial.

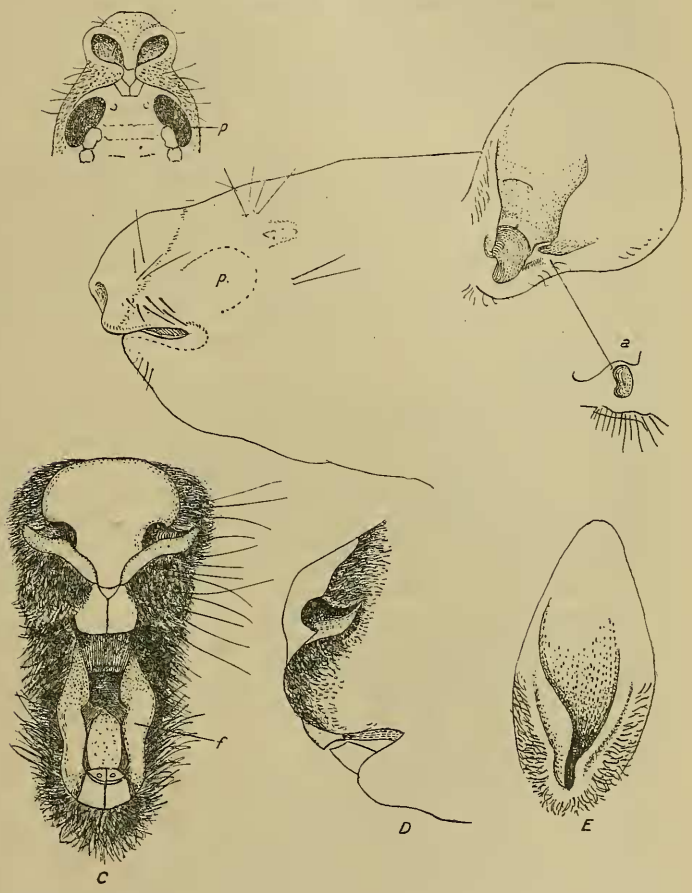
a. A flap of skin jutting inwards from the lower lip and lying alongside the tongue on each side ..... *Phascolomys*.
a'. No flap of skin jutting into mouth from the lips.
b. A cheek-pouch on each side of the upper jaw ..... *Phascolarctos*.
b'. No cheek-pouches ..... *Pseudochirus*, *Phalanger*, *Trichosurus*.

The Ear.—In *Trichosurus* the ear is high, but tolerably narrow and nearly naked internally. The supratragus (metatragus) is a well-developed thick, semicircular, slightly upturned disk. Above it there is a low curved ridge. In front of it the cavity of the ear is defined by a strong oblique ridge passing upwards slightly above the low ridge above described and inferiorly curving backwards beneath the supratragus and passing thence downwards on the inner side of the well-developed tragal thickening forming the anterior rim of the inferior notch (*aditus inferior*), the posterior border of which is defined by a strong thick antitragal ridge, capable of being turned outwards and backwards to a certain extent; but it exhibits no pocket-like depression.

In *Pseudochirus peregrinus* the ear is nearly as naked internally, and relatively nearly as high as in *Trichosurus* but somewhat broader. The supratragus is as well developed, but forms a more distinct roof to the deep lower portion of the cavity. The low

ridge seen in *Trichosurus* is represented by a lobate thickening, and there is a similar thickening lower down behind, above the posterior end of the supratragus. The anterior ridge forms a lobate expansion above the anterior end of the supratragus, and the tragus itself is less well defined. The ridge behind the

Text-figure 23.



A. Head of *Phascolarctos cinereus*, with position of cheek-pouch (*p*) dotted in and pocket of ear (*a*) seen from above.

B. Nose and part of palate of the same, showing the nostrils and the orifices of the cheek-pouches (*p*).

C. Nose and mouth of *Phascolomys ursinus*, with lower incisors cut short and flap of skin (*f*) projecting into monih.

D. Side view of rhinarium of the same.

E. Ear of *Lasiorhinus latifrons*, from dried skin softened in water.

inferior notch turns inwards above towards the posterior end of the supratragus, and it is provided with a shallow pouch defined externally by a definite thickened ridge.

The ear of *Phalanger maculatus* is greatly reduced, thickly covered with hair externally, and scarcely projects above the level of the head. The supratragus is large and valvular, and the cavity of the ear above it is deep and roofed over by a ridge resulting possibly from the confluence of lobate thickenings homologous to the two seen in *Phalanger*. The anterior ridge does not extend so high above the supratragus as in the two genera already discussed, and there is a trace of the pouch on the posterior ridge, although it is not so well defined as in *Pseudochirus*.

In *Phascolarctos* the ear is more expanded even than in *Pseudochirus*, but it differs from the ear of that genus, *Trichosurus*, and *Phalanger* in having the supratragus reduced to a low curved ridge without any trace of the lobe*. There is a low ridge above it as in *Trichosurus*, and the anterior ridge bounding the cavity of the ear in front is as in that genus; the tragus, however, is much smaller. The pocket on the posterior ridge is present as in *Pseudochirus*, but is deeper and has a more sharply defined posterior rim.

In *Phascolomys* the antero-internal ridge, continuous above with the slightly overfolded anterior margin of the pinna, is produced inferiorly into a large compressed lamina, jutting backwards into the cavity of the ear and descending to the auditory orifice. Anteriorly and externally this lamina is marked by a deep groove which descends and passes into a low ridge defining the anterior border of the inferior notch, but there is no definite tragal thickening. The antitragal ridge is also simple. It ascends and forms the posterior edge of the cavity of the pinna, and is itself marked externally and posteriorly by a groove. The supratragus appears to be represented by a low ridge visible above the laminate expansion of the antero-internal ridge.

The ear of *Lasiorhinus latifrons* is very like that of *Phascolomys*, but is longer. On a skin softened in water I could find no trace of the supratragus.

The ear of *Phascolomys* resembles that of *Phascolarctos* in the complete or almost complete disappearance of the supratragus—an important character considering the constancy in the development of this ridge in many Mammals. But in the simple structure of the posterior antitragal ridge it is more like that of *Trichosurus*.

The differential characters of the ear may be used to define and classify the five genera as follows:—

a. Supratragus represented by a strong ridge with well-developed lobate thickening.

b. No pocket above the antitragal ridge .... *Trichosurus*.

* Thomas mentioned this peculiarity and wrote "metatragus almost obsolete."

b'. A pocket above the antitragal ridge.
c. Pinna greatly reduced; pocket small ..... *Phalanger.*
c'. Pinna large; pocket better developed ..... *Pseudochirus.*
a'. Supratragus at most represented by a low curved ridge; without trace of lobate thickening.
d. Antero-internal ridge normally developed; a large pocket above the antitragal ridge ..... *Phascolarctos.*
d'. Antero-internal ridge large and laminate; no pocket above antitragal ridge ..... *Phascolomys.*

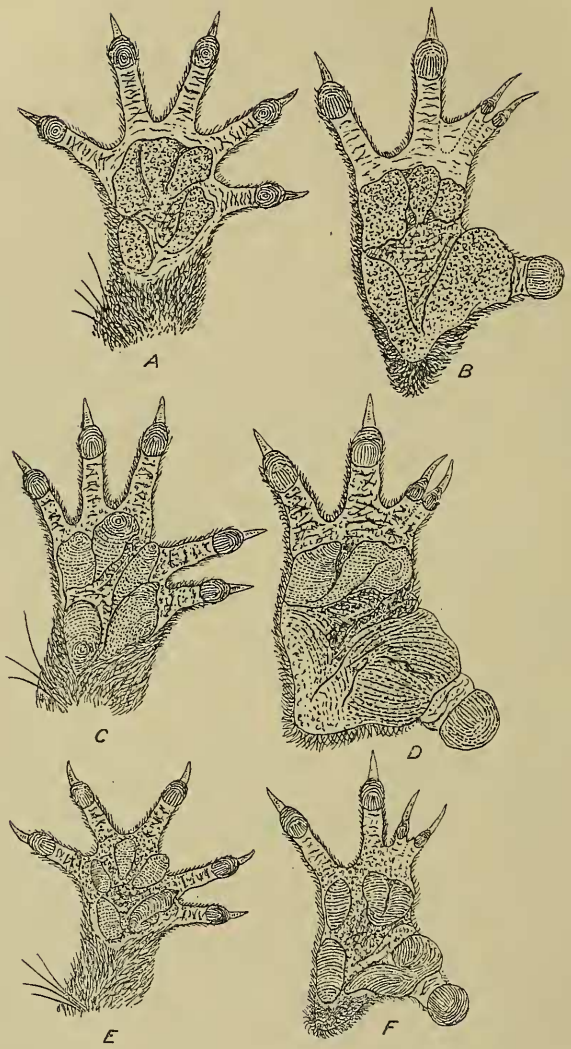
The Fore Foot.—In *Trichosurus*, *Phalanger*, and *Pseudochirus* there is a tuft of long carpal vibrissæ. In *Phascolarctos* and *Phascolomys* these tactile bristles are absent.

In *Trichosurus* the fore foot presents no special modifications. The five digits are free of webbing down to the plantar pads and are nearly evenly spaced, the third and fourth being the longest and subequal, the second and fifth a little shorter but subequal and rising at approximately the same level, and the first or pollex much the shortest, about two-thirds the length of the third or fourth, and not opposable but closing obliquely backwards and inwards across the sole (palm). The claws of all the digits are compressed, curved, and pointed, and the integument of the lower side of the digits is transversely grooved. The uniformly granular plantar pad is four-lobed, the three main lobes being in contact. The inner or pollical lobe, sometimes separated from the main lobes, is fused with the inner element of the carpal pad into a longitudinal mass, longer than wide. The external element of the carpal pad is elliptical, narrowly separated in front from the external lobe of the plantar pad, and, like the internal element, passes imperceptibly proximally into a narrow naked area of skin between them and the hair of the wrist. The centre of the sole is depressed and granular like the pads and the depressions between them.

In *Phalanger* the fore foot is considerably modified from the type seen in *Trichosurus*. The third, fourth, and fifth digits are evenly spaced; but the second is capable of being separated from the third by a much greater space than that between the third and fourth. With the pollex it is capable of being extended almost at right angles to the axis of the foot and of being closed transversely upon the sole. The pads are transversely striate, with the spaces between them granular, the space or groove between the second and third being deeper than that between the third and fourth. The first, the internal or pollical lobe, forms a continuous subtriangular mass, directed obliquely backwards and inwards when the pollex is drawn back, and the external moiety of the carpal pad is larger than in *Trichosurus*.

The capacity for co-operative movement of the first and second digits in a plane nearly at right angles to that of the third, fourth, and fifth seems to have been overlooked in *Phalanger maculatus*. Bensley, at all events, records the similar phenomenon in *Pseudochirus* and *Phascolarctos* as peculiar to these two genera. Nevertheless, the modification in question may be

Text-figure 24.



A, B. Right fore and hind foot of *Trichosurus vulpecula*.
C, D. „ „ *Phalanger maculatus*.
E, F. „ „ *Pseudochirus peregrinus*.
× $\frac{1}{3}$.

clearly seen even on dried skins; and it is shown in the figures of the Spotted Cuscus in the Royal Natural History, iii. p. 257, 1894, and Harmsworth's Natural History, ii. p. 888, 1910. These figures bear the impress of having been drawn from life by Mützel and Kühnert respectively.

The fore foot of *Pseudochirus* resembles tolerably closely that of *Phalanger*, except that the third digit is not lengthened and the lobes of the plantar and carpal pads are separated and smaller, the fused pollical element of the plantar pad and the inner moiety of the carpal pad forming an oblique transverse mass about twice as wide as long.

The fore foot of *Phascolarctos* is an extreme exaggeration of the type seen in *Phalanger* and *Pseudochirus*, although the pads and intervening spaces are areolated or granular, not striated. The sole is much longer as compared with its width: the first and second digits are completely isolated from the rest, and rise close together from the postero-internal angle of the foot, at right angles to its long axis and close transversely across the proximal half of the sole, the posterior border of the pollex when drawn back being approximately in the same transverse line as the posterior border of the sole. There is a large three-lobed plantar pad at the base of the third, fourth, and fifth digits, and there is a similar but smaller lobe upon the base of each of the second and first digits. The one on the pollex probably represents the inner moiety of the carpal pad, and the one on the base of the second digit the first or external element of the plantar pad, widely severed from the lobe in front of it and altogether disconnected from the pollex behind it. The external moiety of the carpal pad is small, restricted to the postero-external angle of the foot and widely separated from the plantar pad.

In *Phascolomys* the fore foot, modified for terrestrial progression and digging, is very different from that of the preceding genera, especially from that of *Phascolarctos*. It may be derived from the type seen in *Trichosurus* by the shortening and widening of the digits and sole, the obliteration of nearly all trace of the individual elements of the pads, and by the straightening, lengthening, and blunting of the claws.

The Hind Foot.—In *Trichosurus**, *Phalanger*, and *Pseudochirus* there are one or two tactile vibrissæ, similar to the carpal vibrissæ, on the inner side of the heel behind the hallux. These are absent in *Phascolarctos* and *Phascolomys*.

The hind feet of the four arboreal genera—*Trichosurus*, *Phalanger*, *Pseudochirus*, and *Phascolarctos*—differ from each other much less than the fore feet. Their general structure is well known. Hence only the comparatively minor points of difference need be noticed.

* Represented in the figure of the hind foot of *Pseudochirus cooki* (pl. 20. fig. 4, of Waterhouse's 'Marsupiata'), but apparently unnoticed in the text.

In *Trichosurus* the conjoined second and third digits* are much shorter than the fourth. The three lobes of the plantar pad at the base of the terminal digits are in contact, the outer lobe being larger than the other two taken together. The large lobe of the hallux shows no trace of division, and there is a tolerably well-defined, long external metatarsal pad reaching from the heel almost to the plantar pad.

The digits of *Phalanger* are approximately as in *Trichosurus*; but the external lobe of the plantar pad is separated to a certain extent in front from the other lobes, which are fused although defined by a groove, and are together larger than the outer lobe. The entire hallux is relatively larger than in *Trichosurus*, and its great pad is indistinctly divided; there is no distinct external metatarsal pad and the heel is shorter than in *Trichosurus*.

In *Pseudochirus* the digits are as in the foregoing genera, but all the elements of the striated pads on the sole are better defined even than in *Trichosurus*. The outer lobe of the plantar pad is completely isolated from the two conjoined inner lobes and about half their size. The great pad of the hallux is distinctly divided, into a distal and a proximal portion, the latter representing the inner metatarsal pad; the outer metatarsal pad is well developed, sharply defined, and about twice as long as wide.

In the foregoing genera the hind foot is larger in every way than the fore foot.

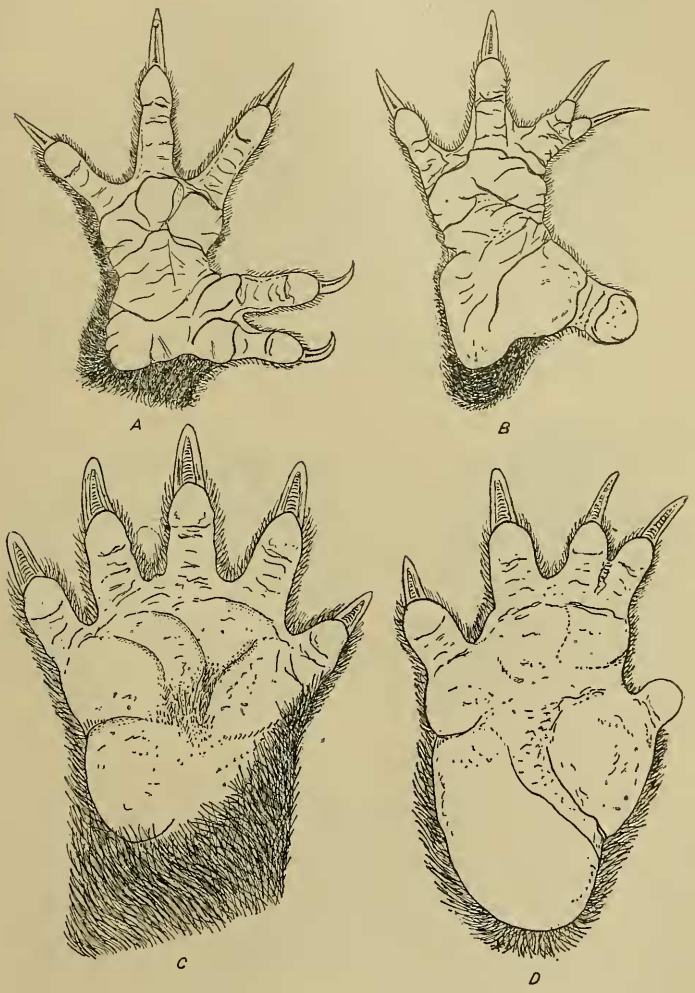
In *Phascolarctos* the hind foot is not larger than the fore foot. It differs from the hind foot of the other genera in having the united second and third digits relatively much longer and only a little shorter than the fourth; the lobes of the plantar pad are feebly differentiated, being fused to form a transverse cushion, with irregularly convex anterior and irregularly concave posterior border. The great pad of the hallux is undivided, and there is no distinctly defined external metatarsal pad. Thus in the development of the pads the foot of this genus differs more from that of *Pseudochirus* than from that of *Trichosurus*.

The hind foot of *Phascolomys*, as has often been pointed out, is a fossorial modification of the Phalangerine scansorial hind foot, resulting from the conversion of the sharp, curved claws of the latter into longer, stronger, and straighter claws, from the approximate equality in length between the fourth and the united second and third digits, the reduction in bulk of the great pad of the hallux so that it projects only slightly beyond the inner margin of the foot, with the terminal segment of the digit planted like a hemispherical tubercle upon it, and from the practical

* These two united digits act as a fur-comb in Marsupials. Possibly they were primarily modified for that function. Generally they are too small in arboreal forms to be of much use for grasping. But this cannot be maintained in the case of *Phascolarctos*; and in *Phascolomys* they are large enough to be subservient to digging. But in the Kangaroos they appear to be retained solely for the purpose mentioned, and may frequently be seen to be so employed. Moreover, it is significant that these are the only digits in *Tarsipes* which have other than rudimentary claws.

obliteration of the pads with expansion of the heel; but, as in the Phalangerine foot, the fifth digit is more widely separated from the fourth than the latter is from the third, although the digit in question is relatively shorter and the space above mentioned somewhat wider.

Text-figure 25.



A, B. Right fore and hind foot of *Phascolarctos cinereus*.
C, D. „ „ *Phascolomys ursinus*.
$\times \frac{1}{2}$.

By their feet the genera may be distinguished as follows:—

a. Feet fossorial with digits short, claws long, blunt and slightly curved, and the granular pads but little differentiated; hallux short, its distal phalange reduced to a button-like excrescence on the shortened lobe, which, however, still retains the capacity for movement in the opposable plane ... *Phascolomys.*

a'. Feet scansorial and prehensile, with longer digits and sharp, curved claws, and differentiated pads; hallux very large and opposable, with well-developed terminal phalange.

b. Fore foot as large as hind foot, with comparatively long and narrow sole; the inner lobe of the plantar pad small and attached to the base of the second digit, which is separated by a long space from the third; the inner lobe of the carpal pad small, isolated from the outer and attached to the base of the first digit (pollex); second and third digits of hind foot comparatively large, strongly prehensile ..... *Phascolarctos.*

b'. Fore foot smaller than hind foot, with shorter, broader sole; the inner lobe of the plantar pad large, in contact, or nearly so, with the rest of the pad and fused into one mass with the inner lobe of the carpal pad, there being no differentiated pad at the base of the first digit (pollex); second and third digits of hind foot short, weakly prehensile.

c. A comparatively long space between the third and second digits of the fore foot, the second acting in unison with the first like a double opposable pollex; pads striated ... *Phalanger* and *Pseudochirus.*

c'. The five digits of the fore foot evenly spaced, the second in no respect opposable to the next, and the first or pollex only slightly so; pads granular..... *Trichosurus.*

The Pouch.—I have seen no fresh female examples of *Phalanger* and *Pseudochirus.*

In *Trichosurus* the pouch, as in *Macropus*, is deeper than wide, its orifice has a well-developed lateral and posterior rim but no overhanging anterior rim; it therefore looks forwards *; and in the specimen examined there were only two teats, not four, as stated by Winge to be characteristic of the Phalangeridæ.

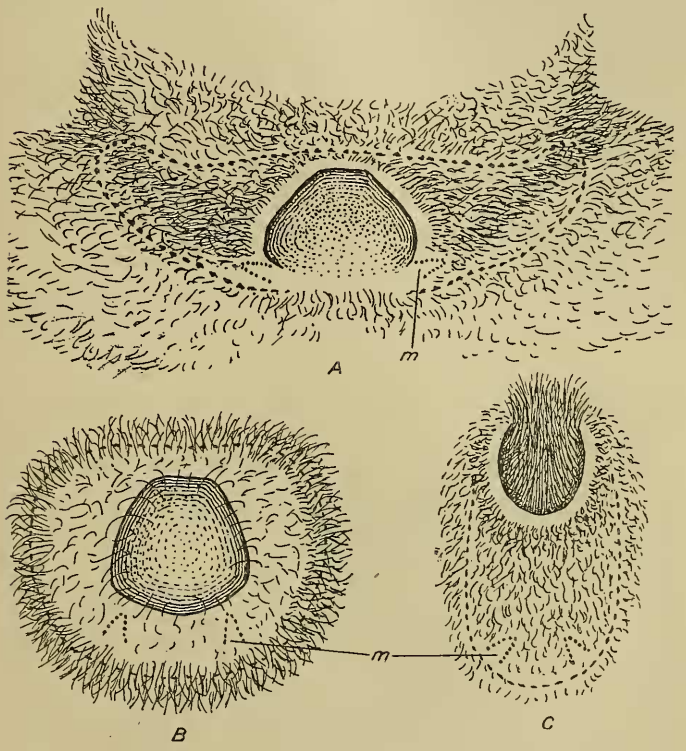
In *Phascolomys* the pouch is a little wider than long, being deeper laterally, especially anteriorly, than behind or mesially in front, and a little deeper behind than mesially in front, the muscular rim overhanging the cavity all round; and there is a single pair of teats.

In *Phascolarctos* the pouch, as recorded by Forbes, is much wider than long, being extended, gradually narrowing as it goes, along the depression between the muscles of the thigh and abdomen nearly as far as the edge of the flap of integument joining the hind leg to the body, its width being about three times its length. The orifice looks slightly backwards, the muscular rim overhanging the cavity laterally and to a slight extent in the middle line in front, but ceasing on each side close to the position of the single teat. The orifice therefore looks backwards.

* In his volume on Marsupials (Allen's Naturalists' Library, p. 76, 1894), Lydekker wrongly states that the orifice of the pouch is directed backwards in Phalangeridæ.

From the description of these three pouches it is evident that the pouch of *Phascolomys* is structurally intermediate in many respects between those of *Trichosurus* and *Phascolarctos*. The differences between the pouches of the last two genera, considering that both are arboreal forms, is remarkable, especially in view of the theory that has been advanced that the anterior upward aspect of the orifice is an adaptation to arboreal life or to the

Text figure 26.



A. Pouch of *Phascolarctos cinereus*.
B. „ *Phascolomys ursinus*.
C. „ *Trichosurus vulpecula*.

The extension of the pouch beneath the integument with the mammæ (*m*) at its posterior end shown diagrammatically with dotted lines.

more or less upright attitude assumed by such terrestrial bipedal forms as *Macropus*, and conversely that the posterior aspect of the orifice is an adaptation to the terrestrial life and quadrupedal gait of such genera as *Thylacinus* and *Sarcophilus*. This theory entirely breaks down in the case of *Phascolarctos*, perhaps the most specialized scansorial genus in the entire order.

The deep, backwardly directed pouch of *Trichosurus* seems so well adapted for the safe retention and carrying of the young up in the trees that its replacement by a laterally directed pouch with the orifice opening towards the tail, such as is seen in *Phascolarctos*, seems most unlikely. The use of the lateral extension for lodging the young carried by a mother who doubtless climbs at times head-downwards is easy to imagine, but the reason for the reversion of the orifice demanded by the theory of the descent of *Phascolarctos* from the Phalangerine stock is puzzling. The structure of the pouch alone supplies evidence that *Phascolarctos* is not closely related to any genus of the Phalangeridæ.

The characters of the three types of pouches above described may be summarized as follows :—

a. The orifice, not encircled behind, opening backwards and downwards; cavity of pouch extended laterally on each side along the depression between the thigh and the abdomen ..... *Phascolarctos*.

b. The orifice subcircular, surrounded by a flap of skin all round; cavity subcircular, a little deeper laterally than elsewhere ..... *Phascolomys*.

c. The orifice opening forwards, at the anterior end of the cavity, which is longer than wide ..... *Pseudochirus*, *Phalanger*, *Trichosurus*.

The Classification of existing Diprotodonts.

My opinion on the classification of the Diprotodonts is as follows :—

1. Winge's removal of *Phascolarctos* from the Phalangeridæ must be accepted. But although that genus shows points of resemblance to *Phascolomys* not shared by other existing Diprotodonts, the differences between them are too many and too important to admit of their ascription to the same family. Moreover, if we adopt as criteria of family rank such characters as those distinguishing the Kangaroos from the Phalangers, the characters separating the Koala and the Wombat should, I think, be given superfamily rank indicated by the titles Phascolarctoidea and Phascolomyoidea. Assuming Winge to have correctly placed the extinct forms above referred to, the Phascolarctoidea will contain the two families Phascolarctidæ (*Phascolarctos*) and Thylacoleonidæ (*Thylacoleo*); and the Phascolomyoidea the two families Phascolomyidæ (*Phascolomys*, *Lasiorhinus*, *Phascolonus*) and Diprotodontidæ (*Diprotodon*, *Nototherium*).

2. The two above-mentioned superfamily groups are individually equivalent to a group of that rank, containing the rest of the Diprotodonts, for which two names are available, Hypsiprymnoidea and Phalangeroidea. I prefer the latter on account of its greater familarity and its derivation from the name of a more primitive genus. Accepting for this group Thomas's families Macropodidæ and Phalangeridæ, it seems clear in the case of the former that if the characters of *Potorous* and its allies entitle

them to rank as a subfamily—and I see no reason for dissenting from that view,—the characters of *Hypsiprymnodon* must be given the higher rank of a family, the Hypsiprymnodontidæ equivalent to, and standing between, the Macropodidæ and the Phalangeridæ, but not definitely assignable to either.

From the typical Phalangeridæ constituting the subfamily Phalangerinæ, the genera *Pseudochirus* and *Petauroides*, characterized by the crescentic pattern of the molar teeth, may be separated as the Pseudochirinæ as proposed by Winge. But it does not appear to me that proper appreciation has been shown for the characters of the very highly specialized genus *Tarsipes* *, which differs profoundly from the Phalangeridæ in the structure of the skull, teeth, tongue, snout, and alimentary canal, as Thomas recorded. The genus seems to be at least as widely divergent from the Phalangeridæ as are the Macropodidæ. These two families, indeed, are linked by the Hypsiprymnodontidæ, and the evolutionary stages by which the Kangaroos have been derived from the Phalangerine stock may be traced with reasonable certainty through living forms. But all the hypothetical intermediate genera between *Tarsipes* and the Phalangers have died out, leaving that genus isolated. And since, in my opinion, it differs more from the typical Phalangers than do the Pseudochirines, it may be raised at least to the rank of a family—Tarsipedidæ.

Briefly, the existing genera of Diprotodonts may be classified as follows:—

Phalangeroidea.

Fam. Macropodidæ.
Subfam. Macropodinæ.
,, Potoroinæ.

Fam. Hypsiprymnodontidæ.

Fam. Phalangeridæ.
Subfam. Phalangerinæ.
,, Pseudochirinæ.

Fam. Tarsipedidæ.

Phascolarctoidea.

Fam. Phascolarctidæ.

Phascolomyoidea.

Fam. Phascolomyidæ.

* Winge and Bensley even considered the characters of this genus to be of less systematic value than the concentric molars of *Pseudochirus*.